BOTANICAL GAZETTE

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On Monilia fructigena.

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WITH PLATE VII.

During the past fifteen years or more, attention has several times been directed, especially by American writers, to a parasitic fungus which causes great destruction of the fruits of certain cultivated *Rosaceæ*, chiefly *Pruneæ* and *Pomeæ*. It is most common on the stone-fruits, so that the affection to which it gives rise is ordinarily known in America as the "brown rot of stone-fruits." This fungus has been called by most recent writers *Monilia fructigena* Pers., but was earlier known as *Torula fructigena* Pers., *Acrosporium fructigena* Pers., *Oidium fructigenum* Lk., *Oidium laxum* Ehr., *Oidium Wallrothii* Thüm., and *Oospora fructigena* Wallr. It appears to have been first named *Torula fructigena* by Persoon[1], and was subsequently transferred by him[2] to the genus *Monilia*.

The plant was for a long time regarded as a saprophyte and von Thümen[3] and Hallier[4] seem to have been the first to point out its economic importance. Thümen subsequently[5] discussed its effects more fully, bringing out more prominently the evidence for its truly parasitic nature, and its claims to be regarded as a disease-producing organism. Yet the chief handbooks of plant diseases pass it with very brief mention or with none, and, even at present, it does not appear to be recognized in Europe as a source of loss to the extent that is fully justified by its ravages in America. Here it was first described by Peck,[6] in 1881, and by Arthur,[7] in 1884.

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[1] Observ. Mycol., 1: 1796.

[2] Syn. method. Fung., p. 693: 1801.

[3] Oesterr. landw. Wochenbl., 1875, n. 41, p. 484.

[4] Wiener Obst- u. Garten-Zeitung, 1876, p. 117.

[5] Fungi Pomicoli, p. 22: 1879.

[6] 34th Rep't N. Y. State Museum, p. 35. See also 43rd Rep't do. p. 6.

[7] 4th Rep't N. Y. Agr. Exp. Sta., p. 254.

Subsequently its structure, as well as its disease-producing capacity and its means of dissemination and survival, have been studied by Galloway,[8] Smith[9] and the writer.[10] Various other accounts of its attacks, with recommendations as to the best means of avoiding them, have been published, chiefly in experiment station literature, and need not be more precisely quoted here. Neither need the results of studies bearing on the prevention or avoidance of the ravages of this fungus be discussed, since our present concern is with its structural relations.

The fungus, which, as Galloway[11] and Smith[12] have shown may attack foliage and young branches, as well as fruits, appears externally in the form of ashy tufts. Each tuft consists of a very large number of threads breaking through a common rift in the surface, and extending to a short distance in either direction from this center. These threads are much branched and consist of chains of ovate or oval thin-walled bodies, strung together in moniliform rows, which may be termed, in a general sense, spores (fig. 1).

The spores are formed, not by successive basipetal constrictions of a hypha, which has previously reached a determinate length, but by repeated budding in basifugal succession, so that the terminal joint or spore is the newest. Occasionally a joint may broaden at its end so that it has two apical angles, and may then produce a bud from each of these angles (fig. 2), thus giving rise to the dichotomous branching of the thread. It is in this way that the branches always originate. After the formation of a thread of greater or less length, according to circumstances, the separate joints or spores mature, and then separate from each other very readily. Thus, while the growth of the threads is indeterminate, their length does not become great in nature, apparently because the influence of the weather is to hasten their breaking up. But in a moist chamber, where these disintegrating forces are less active and the conditions favor very rapid growth, they may become extremely long.

The internal mycelium of the fungus consists of septate cylindrical hyphae, which ramify through the tissues of the

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[8] Rep't U. S. Dep't Agr., 1888, p. 349.

[9] Journ. Mycol. v, 123, and vii, 36. 1890 and 1892.

[10] 8th Rep't Mass. Agr. Exp. Sta., p. 213: 1891.

[11] Loc. cit.

[12] Loc. cit.

host, and, breaking finally through its surface in fascicles, pass directly into the external spore-threads.

The mature spores germinate readily under the influence of warmth and moisture, and produce short threads which ordinarily perish after a few days in water that contains no available nourishment beyond that stored up in the spore. In a natural or artificial nutrient substratum the germ-tubes grow rapidly, penetrating and ramifying through the substratum and soon breaking out through its surface in tufts of spore-threads. Since the spores germinate so readily and are so thin-walled, it has been assumed that their vitality is of brief duration and that they constitute a so-called conidial stage of some fungus, perhaps one of the *Ascomycetes*. Woronin has suggested[13] that it may bear such a relation to some *Sclerotinia*. In the absence of knowledge of its affinities it has been classed among the imperfect fungi, being placed by Saccardo[14] in his *Mucedineae amerosporae*.

Smith has lately observed[15] that the spores retain their vitality, at least in some cases, for a long time; and both he and the present writer[16] have found that the dried tissues of fruits spoiled by the fungus contain a resting mycelium (fig. 3), and even definite thick-walled resting bodies or *gemmae* (fig. 4), probably developed from the mycelium. These resist long periods of unfavorable conditions and promptly give rise to new spore chains on the return of conditions favorable to vegetation. Thus, when a fruit that has been "mummified" by the fungus is gathered in winter or early spring, it commonly sends out new spore-chains of the *Monilia* type, on being placed in the moist chamber. And the same thing occurs spontaneously in nature when the weather becomes warm and damp enough, later in spring. These facts do away with a necessity for any other stage in the history of the plant and make it possible to believe in the autonomy of the form under discussion.

This, in brief, is the present status of our knowledge of the fungus. It is the object of this paper to describe and discuss the significance of certain previously undescribed structures

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[13] Mém. Acad. Sci. St. Petersburg, VII. xxxvi, no. 6: 1888.
[14] Sylloge Fungorum, iv, 34.
[15] Journ. Mycol. vii, 36; 1892.
[16] Loc. cit.

that have been met with in the course of a series of cultures of the form. When a mummied fruit is placed in the moist chamber, it not infrequently happens that it fails to produce spore-chains, and to the unaided eye gives little evidence of any change. This occurs especially in late fall, soon after the cessation of vegetative activity. But if the surface of such a fruit be examined microscopically, it will usually be found that the mycelium of the fungus has given rise to immense numbers of closely-set, flask-shaped sterigmata, reminding one of those of *Aspergillus*. Each of these produces at its outer or neck end small globular spores of about 3μ in diameter, every one of which contains a conspicuous oil globule. One rarely finds more than one of these attached to the sterigma, but their vast number and the occasional observation of several still united shows that they must be produced in chains, like *Aspergillus* spores.

When some of these spores are sown on nutrient gelatine they germinate readily, first swelling to double their former diameter, and produce abundant mycelia (fig. 8). After a few days hyphae emerge from the surface of the gelatine and develop typical *Monilia* chains, thus demonstrating the specific identity of the two spore-forms. It is noticeable that these much condensed globular spores increase largely in volume on taking up nourishment, while the *Monilia* spores, originally much larger, undergo no increase in size.

A culture made in the fall of 1890, on prune-gelatine, with *Monilia* spores, at first produced the usual spore-chains and continued to grow until the nourishment contained in the small drop of gelatine was exhausted. At the end of a month from the beginning of the culture, during the whole of which the atmosphere of the moist chamber had been hardly at all disturbed, it was found that some of the chains remained still quite long, while some had broken up spontaneously into their constituent joints. Numerous separate spores lay about upon the surface of the shrunken and exhausted gelatine film or upon the supporting glass slide. Both of these surfaces were only slightly moist, but a number of spores were found to be germinating upon them. That they were the *Monilia* spores cannot be doubted, since they agreed completely in all respects with those still in chains near by. But under the conditions presented, of moderate moisture, lack of nourishment, and perhaps others not recognized as important, the germination was quite different from the usual form. Each spore gave rise, from any part of its surface, to a single germ-tube, or very rarely to two, which became cut up by a few transverse septa. In most cases one or more of the basal cells remained sterile, while some or all of the others produced one or two flask-shaped outgrowths each. At the top of the neck of the flask were formed, in each case, globular spores, 2.5 to 3μ in diameter, of which not more than one was ever seen attached (fig. 6). These spores were also found fallen from their attachments and beginning to germinate (fig. 6, *a*). In other words, these germ threads from the *Monilia* spores produced precisely similar structures to those which we have seen to be sometimes produced by the resting mycelium at the surface of the natural substratum. While these spores can germinate without nourishment, they suffer no preliminary increase in size. On prune-gelatine they swell and germinate as above described. Though their development could not be followed through, there is no reason to doubt that it agrees with that already outlined for this spore-form.

On another occasion, a stout hypha in a culture on prune-gelatine was observed to produce, at the ends of short branches and on slight outgrowths from its sides, long chains of similar globular spores. In this case the spore-chains, having been quite undisturbed, could be plainly recognized, though they readily fell into short sections or into their component spheres (fig. 7). In spite of the absence of distinct sterigmata, it seems probable that this is essentially the same form as the previously described one, since the spores are produced in the same way, are of about the same size, and contain the characteristic oil-globules.

When *Monilia* spores are sown directly upon the surface of nutrient gelatine, they quickly develop a mycelium and spore-chains, as has been said. Several times I have observed, in cases where some spores had been sown a short distance beyond the edge of the gelatine drop, that the threads from them, growing slowly toward the drop, when they finally reached it began, as was to be expected, to grow much more rapidly. But, instead of remaining naked threads, they produced, by a sort of budding from various points or from nearly all points along their sides, oblong bodies, as shown in fig. 5. Sometimes these bodies were far more abundantly produced than is shown in the figure, so that they almost completely filled the gelatine over considerable areas. Unfortunately, their future fate and their capacity for germination were not determined; but that they belong to the *Monilia* cannot be doubted, since the threads which gave rise to them were seen to originate from *Monilia* spores in pure culture and the same threads were traced through the gelatine to points where they emerged from the surface and became *Monilia* chains.

In examining the significance of the phenomena described, we are led first to ask how the various structures described are to be regarded. It is evident that the spores of the *Monilia* chain are not conidia in the truly morphological sense in which Brefeld uses[17] the term. That is, they are not spores produced in fructificative fashion on specialized spore-bearing threads. They are simply slightly individualized portions of mycelium with the form and physiological characteristics of spores. Though differing in the details of their development from the spore-chains of the *Erysipheæ* which constitute the old genus *Oidium*, they are morphologically similar to them. And indeed, as above noted, some writers have included the present plant under that generic name. As Brefeld has shown, all these "Oidien-ketten" are to be regarded as the simplest type of chlamydospore formation. A consistent terminology will, then, designate the common spores of *Monilia fructigena* as chlamydospores of the most primitive type, for which we may retain the name *Oidium*. But the name must be understood in a morphological and not in a systematic sense.

In view of the incompleteness of our knowledge of the oblong bodies described last and shown in fig. 5, it seems best merely to record their occurrence and to await fuller information as to their early and subsequent history, before attempting any discussion of their significance. While it seems probable that they have reproductive capacity, there is little evidence on this point either from their own development or from analogy, since one hesitates to homologize them fully with other described organs of fungi.

On the other hand, the spores of the second form above described are produced on distinct, if short, sporophores and

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[17] Unters. aus dem Gesammtgeb. d. Mykol., 7, 244. This clearly marked and fundamentally important distinction between the conidium and the chlamydospore must be generally recognized.

constitute a true fructification. They are, in any point of view, to be called conidia. Furthermore, the homologies of this form seem to be clear. Tulasne[18] has figured similar structures which he observed on the mycelia of *Peziza (Sclerotinia) tuberosa* and of the closely related *P. bolaris* and *Durieuana*. Brefeld[19] has found them in his cultures of *Sclerotinia tuberosa* and *Libertiana*, and DeBary[20] has seen them in the latter species and *Scl. Fuckeliana.* Zopf[21] saw very similar structures on the mycelium of *Chaetomium*, and Woronin[22] in *Sordaria*. In all of these cases the general structure and mode of development of these conidia is the same. Tulasne found them rather sparingly produced on young germ-tubes developed without extraneous nourishment, just as did the writer in one instance. Brefeld and DeBary obtained them very abundantly in cultures on nutrient media, which was once the writer's experience. When developed from a resting mycelium, they are produced almost as abundantly as on nutrient media. Neither of the writers mentioned above was able to observe the germination of these spores, and they were classed by DeBary[23] as "doubtful spermatia," under the influence of his well known views concerning the typically sexual character of the *Ascomycetes*. It is certain, however, that the conidia associated with *Monilia fructigena* germinate readily and produce a mycelium and *Monilia* chains, as above described. This fact makes it probable that the corresponding forms associated with other fungi, especially with *Sclerotinia* species, are also to be regarded both morphologically and physiologically as microconidial stages, although the conditions of their further development still remain unknown.

In his study of the several species of *Sclerotinia* which attack the leaves and fruits of European *Vaccinium* species, Woronin[24] found a chlamydosporic stage of *Scl. Vaccinii* that very closely resembles that long known as *Monilia* or *Torula fructigena*. His form is in some respects more highly differentiated than the latter, especially in its development of

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[18] Selecta Fungorum Carpologia, III, t. 22: 1865.

[19] Bot. Unters. über Schimmelpilze, IV. 113; t. 10: 1881.

[20] Comp. Morph. and Biol. Fungi: 1884; Eng. trans., 243.

[21] Nova Acta A. C. L.-C. N. C. XLII, no. 5: 1881. Also, Die Pilze, 453: 1890.

[22] Beitr. z. Morph. u. Phys. d. Pilze, III: 1870.

[23] Loc. cit.

[24] Ber. d. D. Bot. Gesell., III, p. lix: 1885. Also, Mém. Acad. Sci. St. Petersburg. VII. XXXVI, no. 6: 1888.

cellulose plugs between the spores, which by their growth force the spores apart and so serve to disseminate them. This plug, called by Woronin the disjunctor, is not in any way represented in *M. fructigena.* Yet the whole habit of growth and the general mode of spore-formation is so similar in the two forms as amply to justify Woronin's suggestion of their possible near relationship. The probability of the correctness of this idea is still further increased by the observation of the microconidial stage above described, although none such is mentioned by Woronin as belonging to either species of the group of *Sclerotinia Vaccinii.* For the occurrence of such a stage in the commonest and best known species of *Sclerotinia* with conidia of the *Botrytis* type[25] affords ground for the belief that another species possessing it may be a *Sclerotinia*, also; and the combined evidence of the microconidial and chlamydosporic stages is very strong. Assuming for the moment that the forms above described are imperfect stages of a *Sclerotinia*, the microconidial form connects the two groups of the genus in an interesting way, bringing more closely together those possessing macroconidia of the *Botrytis* type and those whose "summer-spore" stage is a chlamydosporic one of the *Monilia* type.

As to the actual existence of a perfect form of *Sclerotinia* to which our *M. fructigena* belongs, it can only be said that in the examination of a very large number of fruits in all stages of disease from the attacks of *Monilia*, at all seasons, the writer has never seen any trace of sclerotia or spore-cups; nor have any such been mentioned by other writers. It seems, therefore, pretty certain, in view of the attention that the fungus has received in recent years, that the development of such structures is exceedingly rare, at least. As has been pointed out above, the fungus commonly perpetuates itself by means of its resting mycelium, and the development of sclerotia is therefore wholly unnecessary to the preservation of the species. One may therefore be quite justified in the belief that in *Monilia fructigena* we have the persistent chlamydosporic and microconidial stages of a *Sclerotinia* allied to *S. Vaccinii*, whose perfect stage has become practically or entirely suppressed.

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[25] I shall show in the forthcoming report of the Massachusetts Agricultural Experiment Station that it is probable that *Scl. Libertiana* possesses such a conidial form.

I have not been able to examine the large number of forms included by Saccardo under *Monilia.* Of these it is probable that many have no real affinity with that above discussed; while others may be closely related. Such appears to be the case with a rather common form which attacks the immature fruits of *Prunus serotina* and related species, forming delicate white tufts, with spores very like, but somewhat smaller than those of *M. fructigena.* This is probably the plant called by Saccardo[26] *Monilia Peckiana*, var. *angustior.* The few cultures I have been able to make have yielded only the common spore-chains, but the form will probably repay further investigation as to its pleomorphism and its affinities.

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EXPLANATION OF PLATE VII.

Fig. 1. Two *Monilia* hyphæ passing into branching spore-chains. ×540.

Fig. 2. The end of a spore-chain, showing the origin of branching from two terminal angles of the terminal cell. ×540.

Fig. 3. Bits of resting mycelium from the flesh of a "mummied" plum. ×540.

Fig. 4. Resting cells, "*gemmae,*" from the same source. ×540.

Fig. 5. Hyphæ from *Monilia* spores, with oblong bodies developed within the gelatine. *a*, ×540. *b*, ×940.

Fig. 6. Three *Monilia* spores producing germ-tubes with sterigmata and microconidia. *a*, germinating conidia. ×940.

Fig. 7. Chains of microconidia from *Monilia* hypha, in culture. ×540.

Fig. 8. Microconidia germinating on nutrient gelatine. *b*, after one day, ×940. *a*, after 2 days, ×540.

Non-parasitic bacteria in vegetable tissue.[1]

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It has been ascertained that the tissues of the animal body in their normal healthy state are perfectly free from bacteria but the evidence that the same is true in regard to vegetable life is not so unanimous. The subject has received considerable attention at the hands of bacteriologists and while the majority of observers do not admit that bacteria are to be found in vegetable tissue in a healthy state, some proof has been brought forward to support such a conclusion[1].

In a course of experiments, which have been carried on for

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[26] Sylloge Fungorum, IV, 34.

[1] Read at the Rochester meeting of the A. A. A. S., August, 1892.